Review

"Diatoms: Life in Glass Houses" revisited: Updates and Comments

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ABSTRACT. The film "Diatoms: Life in Glass Houses", produced in 2003, covers various aspects of this ecologically important class of algae, such as their occurrence, cell biology including cell division and reproduction, morphology, morphogenesis, motility, and the formation of colonies. The aim of this work is to review and comment on some of the aspects presented in the video in the light of current knowledge. Special attention will be given to the constraints imposed by the solid silica wall and how diatoms cope with them. No attempt is made to be comprehensive.

Keywords: diatomaceous earth, cell walls, centrics, pennates, microtubule center, motility, phototaxis, mitosis and cleavage, valve and spine morphogenesis, sex in pennates

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Preface

The Cytographics film *Diatoms: Life In Glass Houses*, is a true testament to the scientific love and passions of its creator, Dr. Jeremy Pickett-Heaps. His excitement for all things algal was evident to all of his colleagues and students, and he seemed to have a special interest in the diatoms. Their cell wall morphogenesis, their method of chromosome separation and spindle formation during cell division, and their unique manner of cell movement - they all were fascinating to Jeremy.

One of Jeremy's biggest goals in the lab was to make high resolution detailed observations of cell phenomena, in both real-time recording and electron microscopy, in order to, in his words, "let the cells themselves tell you about what they are doing". For his live and time-lapse filming he used high resolution optical microscopes fitted with 16mm film cameras, photo cameras, and video cameras. He often put the cells into specialized hand-made cell chambers or mounted the cameras or lighting on numerous types of handmade platforms and brackets to get that perfect orientation for the shots. The entire filming room even had the ability to be cooled down if necessary in order to film cells that needed to be kept in cooler environments. Jeremy also had a never-ending desire to present these observations in a way that would generate the most interesting, beautiful, and instructional educational tools. His formation of the company Cytographics with his wife Julianne to produce high-quality educational films merged all of these aspirations.

This film explores many aspects of diatom behavior, using live and scanning electron microscope observations made in his lab, and demonstrates the enthusiasm Jeremy had for these beautiful cells and their unique forms of cellular behavior. It is the hope of the authors that this paper will expand upon the original presentation by discussing some of the information and observations that have emerged since the video's initial release, and reignite some of the excitement and awe for these cells in a new generation of scientists.

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1. Introduction

Twenty one years ago, biologist Dr. Picket-Heaps published a teaching video, *Diatoms: Life in Glass Houses* (Pickett-Heaps, 2003; Pickett-Heaps and Pickett-Heaps, 2022), shedding light on the fascinating world of diatoms - one of the most abundant and diverse groups of photosynthetic microalgae. These remarkable organisms play a pivotal role as primary producers in aquatic ecosystems. Their intricate amorphous silicon dioxide shells, known as frustules, are adorned with ornate and porous features (Round et al., 1990). The frustules are eponymous for this movie, and hence it can be expected that they play an important role in it – as they may also do for the organism, although this aspect is still widely unknown and debated today (Goessling et al., 2024). As we commemorate the anniversary of this publication, it presents an opportune moment to not only pay homage to Dr. Pickett-Heaps' work but also to reexamine and expand upon its content (Fig. 1) through the lens of contemporary scientific advancements.

Advancements in the field of diatom research over the past two decades have been profound, encompassing some developments that have enriched our understanding of these microorganisms. Researchers have looked into various facets of diatom biology, ecology, and biogeography, uncovering new dimensions of their importance and functionality within aquatic ecosystems (Keck et al., 2016; Soininen and Teittinen, 2019). One notable advancement lies in our comprehension of the molecular mechanisms controlling frustule formation and silica biomineralization (Hildebrand and Lerch, 2015). Additionally, advancements in imaging techniques, such as electron microscopy and atomic force microscopy, have enabled researchers to explore the ultrastructure of diatom frustules with more detail (Luís et al., 2017). Optical microscopy capabilities have been enhanced by the use of special fluorescent dyes that penetrate living cells and stain only growing siliceous structures (see Table 1/ Fig. 3). Furthermore, the field has witnessed a burgeoning interest in the ecological roles of diatoms beyond primary production (Leblanc et al., 2018), including their interactions with other organisms (Amin et al., 2012), contribution to biogeochemical cycles, and responses to environmental changes such as ocean acidification and climate warming (Jin et al., 2024). Studies have elucidated the ecological significance of diatom diversity, distribution patterns, and functional traits in shaping aquatic ecosystems and influencing global biogeochemical cycles (Benoiston et al., 2017). The advent of high-throughput sequencing technologies has expanded and partly updated diatom taxonomy and ecology within this diverse group (Visco et al., 2015; Rimet et al., 2018).

Certain aspects of Dr. Pickett-Heaps' teachings may warrant reevaluation in light of these novel findings and evolving perspectives. For instance, our understanding and thoughts of diatom ecological niches, community dynamics, and responses to anthropogenic stressors has evolved (Behrenfeld et al., 2021; Jin et al., 2024), necessitating a reassessment of the ecological principles governing diatom ecology. There has also been substantial work on the silica structures and genes involved in the process of biomineralization in diatoms (Hildebrand and Lerch, 2015), including identifying genes for cingulins (involved in patterning), silicon transporters (involved in silicon uptake and concentration), and silaffins (silicon biochemistry). Moreover, there is also increasing interest and active work in the applied biology of silaffins to understanding general patterning and formation during biomineralization (Pamirsky and Golokhvast, 2013; Lechner and Becker, 2015). In conclusion, while Dr. Pickett-Heaps' seminal work laid the foundation for our understanding of diatoms with emphasis on reproduction and frustule development, the past two decades have had some advancements in diatom research, spanning molecular biology, ecology, and biogeography, as well as the application of diatom products in modern technologies (Fu et al., 2015). As we reflect on the anniversary of "Diatoms: Life in Glass Houses," it serves as a poignant reminder of the dynamic nature of scientific inquiry and the continuous quest for knowledge in unraveling the mysteries, still existing in our natural world.

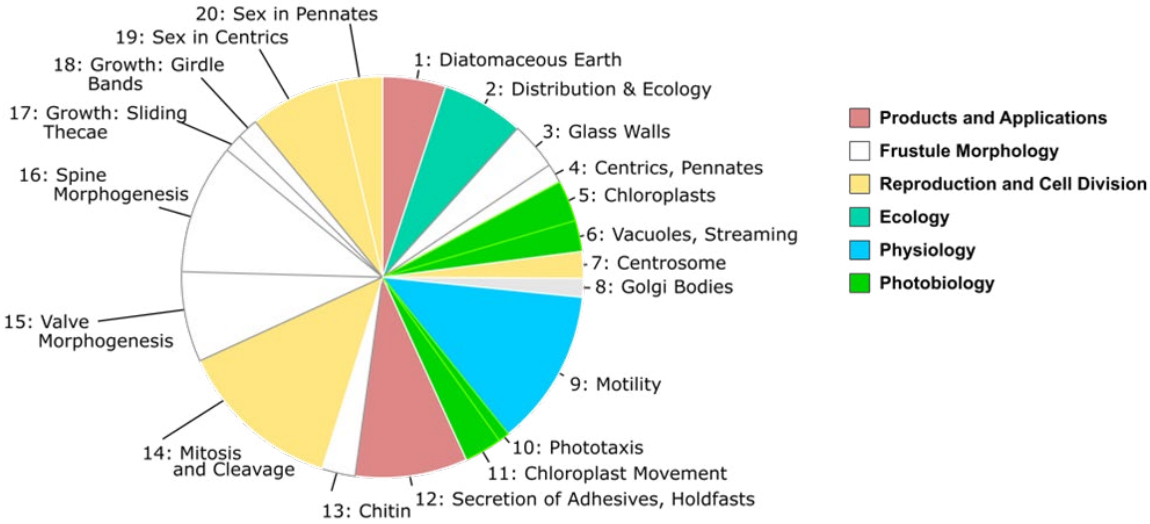

Fig.1. Chapter Analysis of «Life in Glass Houses» Video. The video is segmented into 20 chapters, each exploring various aspects of diatom research. Our color-coded visualization highlights the diverse range of topics addressed by Picket-Heaps, with segment sizes in the pie chart reflecting the duration dedicated to each exploration.

Table 1. Biosilica trackers for the study of diatoms

Substances	λ_{ex}, nm	λ_{em}, nm	Fluorescence quantum yield	Medium	Reference
*Rhodamine 19	525	550	0.63	In water for the cationic form $Rh19H^+$	Arbeloa et al., 1991
*Rhodamine 6G	526	551	0.59	In water	Arbeloa et al., 1991
PDMPO (DND-160)	384	540	0.31	Buffer solution pH 3	Sabnis, 2015
	329	440	0.34	pH 7.7, water	
	338	510	0.38	pH 7, in the presence of silicic acid	Shimizu et al., 2001
HCK-123	485	535	-	pH 7, water	Desclés et al., 2008
NBD-N3	500	551	0.015	pH 7, water	Danilovtseva et al., 2013
NBD-N2	490	554	0.061	pH 7, water	Danilovtseva et al., 2019
Rhod-N3H	465	590	0.134	pH 7, water	Danilovtseva et al., 2019
Q-N2	419	480	0.074	Aqueous silica nanoparticles, pH 5.5	Annenkov et al., 2019
Flunet	455	520	0.279	pH 7, water	Annenkov et al., 2024

Note: * More rhodamines with similar spectral properties are described in (Kucki and Fuhrmann-Lieker, 2012).

Here we provide an update on the field of diatom research, following the sequence of the teaching video provided by Pickett-Heaps. The aim is to review how the field of diatom research developed within the past 20 years, and we take the opportunity to discuss selected aspects from the video within the past development in more detail. In the following text, notes are given on topics where the authors consider that new insights and perspectives have emerged. The notes follow the chapter structure of the film. We would like to mention that the original publication is available with subtitles in different languages (Pickett-Heaps and Pickett-Heaps, 2022). At the time of submission, subtitles are available in English, German, Hebrew, Hindi, Italian, Japanese, Russian, French and Spanish. Others may follow.

2. Results and discussion

2.1. Notes on Chapter 1 "Diatomaceous Earth"

Recent applications beyond the use of Diatomaceous Earth:

The teaching video begins with an airplane ride over Diatomaceous Earth deposits near Lompoc, Southern California, offering insight into the geological significance and widespread distribution of diatoms. This opening segment, though untitled (we here interpret it as Chapter 1, and named it "Diatomaceous Earth"), serves as a fitting introduction, highlighting the historical use of this natural material. In fact, diatomaceous Earth has a history as building material, even influenced prominent structures like the Hagia Sophia, and played a pivotal role in key enabling technologies, including Alfred Nobel's dynamite (Ghobara and Mousa, 2019). While the video touches on previous technological applications of diatomaceous frustules, it is essential to mention also some more recent advancements in its utilization. Contemporary research has revealed properties, such as a low Young's modulus of elasticity (Hamm et al., 2003), Eigenfrequencies (Andresen et al., 2024), hydrodynamic properties (Losic et al., 2006), or slab photonic crystal properties (Goessling et al., 2020b), giving rise for application in bionic frontier and emerging technologies (Rabiee et al., 2021).

The observation that frustules exhibit photonic properties - i.e. light-matter interaction through structural design at nanoscale - has been documented for decades, evident in their colorful appearance under specific lighting conditions, despite being composed of amorphous silicon dioxide, transparent for light in the visible spectral range. However, recent studies have demonstrated that certain frustule components function akin to slab photonic crystals (Fig. 2), owing to their precise nanoscale structure and ability to manipulate light (Goessling et al., 2020b). The groundwork for looking at diatom frustules from this perspective was laid by Fuhrmann et al., 2004, who proposed this concept for the frustule parts (valves and girdle bands) of the species *Coscinodiscus granii* using numerical simulations. Of particular interest is the fact that the concept of slab photonic crystals was developed in the late 1980s (Yablonovitch, 1987), but that these structures may have already existed in the oceans millions, or even hundreds of millions of years before human invention. Slab photonic crystals are characterized by their relatively simple structural configuration, which enables the manipulation of light in up to three dimensions. The periodic nanoscale dimensions are aligned with refractive index contrast and the wavelength of light, resulting in interactions that lead to guided and prohibited light frequencies within the crystal structure. Just 15 years after the initial numerical propositions, slab photonic crystal properties were experimentally confirmed in the girdle bands of the species *C. granii* (Goessling et al., 2020b). It was verified that the structure opens a photonic bandgap in the near-infra-

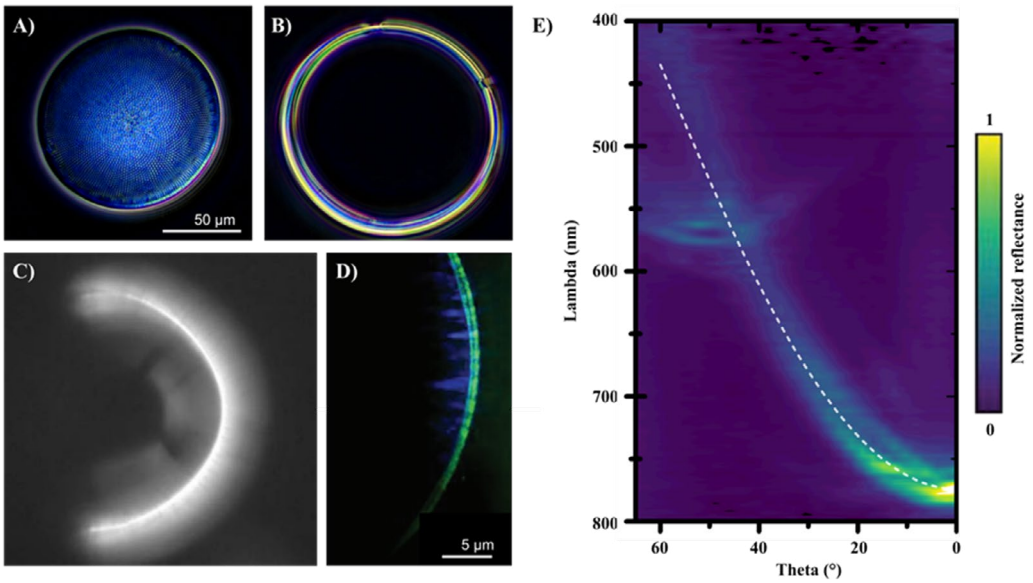

Fig.2. Photonic properties of diatom frustules with potential application in advanced optical technologies. A) Blue iridescence over valves of italicize Coscinodiscus granii, potentially attributed to Mi-scattering across its hexagonal nanoporous structure. B) A dark-field view of the italicize C. granii girdle band. C) Microscopic depiction of a half-girdle band illuminated from the right with white light. The authors observed green and blue-green hues viewed through objective lenses with different numerical apertures. A broad red spot is visible at the focus of the girdle band. D) More recent research experimentally confirmed that girdle bands are slab photonic crystals. E) Fourier-space imaging demonstrating the properties of slab photonic crystals, including reflectance of the photonic stopband, determined as a function of angle of incidence (Theta) and spectral illumination. In water, the stopband occurs in the near-infrared spectral range at normal incidence (Theta = 0˚). The white dashed line shows modelled data based on refractive index approximation. A) and B) are reproduced from (Goessling et al., 2020a). C) is reproduced from (Fuhrmann et al., 2004). D) and E) are reproduced from (Goessling et al., 2020b) under common license agreement.

red spectral range while facilitating light guidance in the green spectral range when immersed in water. Such properties find applications in modern technologies encompassing telecommunication, information, and quantum logic technologies, as well as light harvesting technologies and battery applications (Armstrong and Dwyer, 2015). Frustules have also been proposed as platforms for plasmonic applications, useful, for example, in surface-enhanced Raman spectroscopy and various sensing applications (Wardley et al., 2021; De Tommasi and Chiara de Luca, 2022).

Fluorescent vital dyes

The development of techniques to integrate amine-containing fluorescent dyes during growth has added new properties to the siliceous material and facilitated information about its formation. It was found that rhodamine 123 at a non-toxic concentration could penetrate the frustules, creating fluorescent silica (Li et al., 1989). The idea of using rhodamines in the biotechnological synthesis of highly ordered fluorescent materials was developed in (Kucki and Fuhrmann-Lieker, 2012). A specific disadvantage of rhodamines is the small gap between staining and toxic concentrations. The high quantum yield in aqueous medium made fluorescence microscopy of live cells difficult (need to wash off the dye). In addition to rhodamines, low-toxic dyes with other fluorophore groups have been developed (Table 1), and diatom valves with red, yellow-green, and blue fluorescence can now be obtained (Fig. 3). Fluorescence staining increases our ability to study valves and girdle bands morphology using confocal microscopy.

2.2. Notes on Chapter 3 “Glass Walls”

Are frustules cell walls?

In the video, the term “glass walls”, “walls”, or “cell walls” is frequently used to describe frustules, which are doubtless a type of wall-like structure. However, it is essential to discern whether frustules possess the defining characteristics specifically of cell walls, in biological terms. Traditionally, a cell wall is an extracellular structure, meaning it exists outside the cell membrane. This is the case of the frustule in its final form, as it serves as an extra-cellular barrier or structural support system. Generally, a cell wall acts as a physical barrier against chemical or biological agents, such as bacteria and viruses, and contributes to the structural integrity of the cell (Zhang et al., 2021).

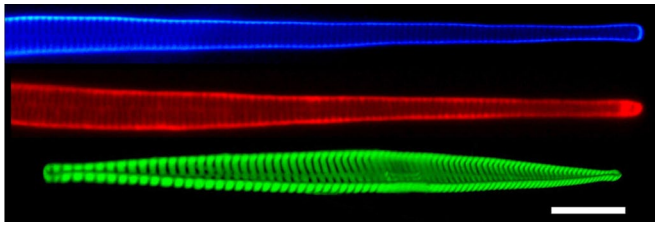

Fig.3. Fluorescence and confocal (bottom) images of different italicize Ulnaria sp. valves after culturing with the addition of dyes (blue: Q-N2; red: Rhod-N3H; and green: NBD-N2; refer to table 1 for references). Developed over the past 20 years, these dyes are incorporated into newly formed frustule parts, enabling the expansion of the range for targeted exploration in experiments requiring specific wavelengths. Experimental details for the doping procedure are available in Annenkov et al. 2019. Scale bar represents 10 µm.

Nevertheless, the formation process of diatom frustules challenges this conventional notion. It is believed that frustules originate, at least partially, within the cell itself, thereby complicating the clear delineation between intracellular and extracellular structures typically associated with cell walls. Although frustules provide analogous functions to traditional cell walls in terms of structural fortification and defense, their unique formation process blurs the distinction between intra- and extracellular domains. Studies have indicated that certain components, such as valves, originate inside the cell (i.e., within the plasmalemma) before being extruded through a yet unidentified mechanism of exocytosis (Hildebrand et al., 2018). Conversely, emerging research indicates that some frustule elements might undergo formation outside the cell (Mayzel et al., 2021).

The nature of this internal formation of wall components followed by secretion to the cell exterior is likely related to similar processes seen in other algae such as chrysophytes in which silicified scales are formed internally then secreted. This internal mineralization and secretion of wall components is typical of several members of the algal silicifiers (Lengyel et al., 2023).

Active regulation of cell buoyancy

Regarding cell buoyancy, an interesting recent observation regarding centric diatom motility has been made, in which the centric cells appear to be able to actively adjust their placement within the water column (Krishnamurthy et al., 2019). While the mechanisms behind this have not been determined, it is possible that some centric cells may be able to actively regulate their buoyancy via osmotic regulation of small changes in cell volume as has been observed in some dinoflagellates (Larson et al., 2023).

2.3. Note on Chapter 4 “Centrics, Pennates”

The use of the terms “centric” and “pennate” in diatom taxonomy, based on DNA sequencing methods

Diatom frustules are generally constructed around one of two types of symmetry: radial and bilateral. This is one of the most obvious characters of a diatom frustule in general, and the two categories of symmetrical organization have largely served as the first dichotomy in their systematics and classification: the “centrics” (radially symmetrical) and the “pennates” (bilaterally-symmetrical). As more diatoms were described and the observational power of available tools increased, so did the number of morphological categories used in their classification, to include radially symmetrical taxa with prism-shaped valves (the “Mediophyceae”) and bilaterally symmetrical taxa with and without paired slits (“raphe slits”) through the valves through which mucilage is extruded for motility (the “Bacillariophyceae” and “Fragilariophyceae”, respectively).

However, even with these additional categories, the core dichotomy has remained. Molecular data, such as DNA and RNA sequence data as well as genome organizational patterns, have suggested this dichotomy is not necessarily reflective of the evolutionary history of diatoms. One of the first attempts to construct a classification of diatoms based on DNA sequence data (Medlin and Kaczmarska, 2004) found that the centric diatoms were not monophyletic (Fig. 4), a result encountered again and again with the addition of more taxa (Alverson et al., 2006, Medlin et al., 2008, Sorhannus and Fox, 2012) and more data (Theriot et al., 2015, Nakov et al., 2018).

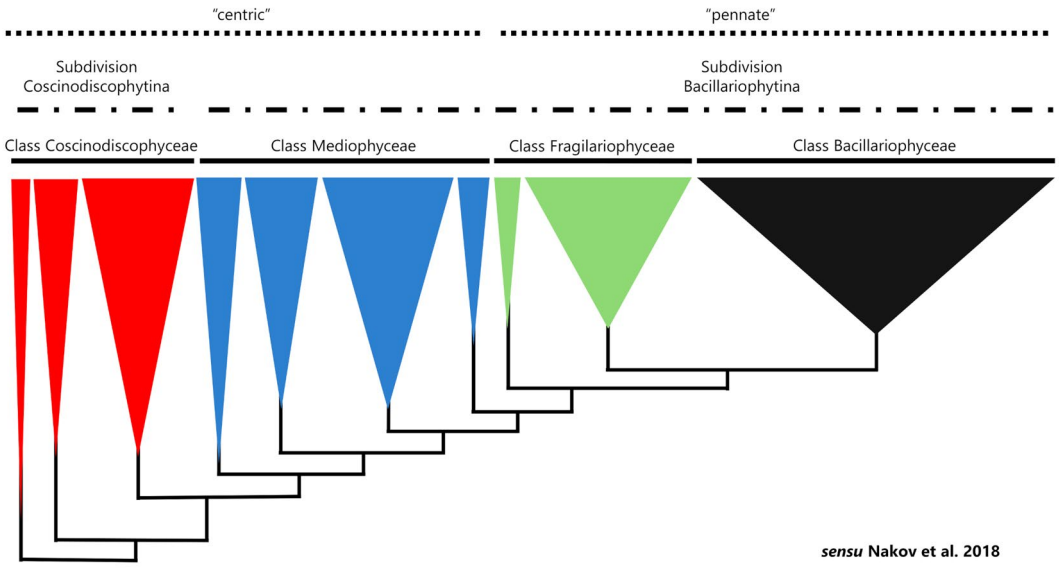

Fig.4. Tree diagram of the molecular phylogeny of diatoms based on Figure 1 in Nakov et al., 2018, a phylogenetic tree based on a concatenated 11 gene dataset from 1151 diatom taxa. The clades are colored by the class designations of Medlin and Kaczmarska, 2004 (labeled above the solid lines). The subdivision taxonomy above the “dot-dash” line is also derived from Medlin and Kaczmarska, 2004, while the classic morphological categories of “centric” and “pennate”, based on valve outline and symmetry, are indicated above the dotted line.

The influence these results have on the utility of the terms "centric" and "pennate" on diatom classification has been debated (Medlin, 2009; Williams and Kociolek, 2010), but one could argue that the use of molecular data has spurred some interest in searching for other characters which diagnose the molecular clades, such as intracellular organization and sexual reproductive characters, discussed below. DNA sequence has supported the hypothesis that "reversals" happen, where taxa which are radially-symmetrical occur in the phylogenetically-derived "pennate" clades. Round and Mann (1980) proposed *Coscinodiscus nitidus* was more closely related to the fragilariophycean pennate *Rhaphoneis* than any centric genus when they transferred the taxon to the new genus *Psammodiscus*, on the basis of the ultrastructure of the valve. DNA sequence data was used to identify a second pennate genus which has regained radial symmetry: *Astrosyne* (Ashworth et al., 2012). This taxon also shares ultrastructural characters with its closest genetic relatives—the pyrenoids of their chloroplasts oriented into a siliceous, circular internal wall—which are bilaterally symmetrical fragilariophyceans. Molecular phylogenetics have also consistently resolved the radially-symmetrical, circular-valved order Thalassiosirales within the clades of the radially-symmetrical, prism-valved Mediophyceae (Medlin and Kaczmarska, 2004, Theriot et al., 2015, Nakov et al., 2018). Clearly, shape and symmetry alone (and the terms "centric" and "pennate") should be reserved for descriptive purposes but not to infer classification or phylogenetic relatedness.

2.4. Note on Chapter 7 "The Microtubule Center (Centrosome)"

Microtubule Centers as universal structures for spatial control of eukaryotic cell structures

As outlined and so beautifully displayed in the film, diatom microtubule centers (centrosomes) are extremely well defined in some diatom species, acting as localization sites and guiderails (via their associated microtubules) for the placement of numerous organelles, and the localization of the spindle in mitosis. The suggestion that diatoms can be useful model organisms to understand such basic cell biology processes has been further validated in the intervening years. Recent studies (Petrova et al., 2023) have used genetic data from a number of diatoms to demonstrate that diatom microtubule centers have a number of components in common with centrosomes from a wide range of plant and animal species, including Aurora A, Centrins, Nucleolins, and Gamma (γ) Tubulin Complexes. These γ-tubulin complexes are thought to be universally crucial to the organization of cell components in eukaryotes (Teixidó-Travesa et al., 2012). The movement and placement of centrosomes and their centrosomal microtubules are responsible for the movement and placement of cellular components and endosomal particles in eukaryotes, mainly via motor proteins such as kinesins and dyneins (Bonifacino and Neefjes, 2017; Hannaford and Rusan, 2024).

2.5. Notes on Chapter 9 "Motility"

Movement of the diatoms of a Bacillaria paradoxa colony

The collective, synchronous movement of *Bacillaria paradoxa* colonies is commented on in the film as follows: "Presumably, their motility system responds to a communal signal, which synchronizes movement and ensures that it occurs in one direction in all the cells and then in the other." First, the direction of movement of diatoms in colonies in a steady state is considered. More complex movement sequences occur when, for example, after switching on a light, resting colonies show a transient oscillation before they move synchronously. The alternation of expansion and contraction is typical for smaller colonies as they can be seen in the movie. There is a period during which the colony remains in a stretched state. Then, the diatoms begin to move relative to their neighbors, with the movement often starting with the diatoms at the ends of the colony. The diatoms begin to move one after the other. There is therefore always a small time delay between the relative movements. The colony contracts and expands until it comes to rest again. The direction of movement is then reversed, and the colony returns to its original position through contraction and expansion. Fig. 5 shows such a colony shortly after it has started to move. The outer diatoms have already begun to move.

A characteristic feature of small, synchronously moving colonies is that the relative movements are never in opposite directions. The synchronous back-and-forth movement of the entire colonies has been described in particular by Kapinga (1989), Kapinga and Gordon (1992), and Ussing et al. (2005).

When the displacements of neighboring *Bacillaria* diatoms are recorded using a tracking method, similar trajectories are found for all diatoms except for a phase shift. With regard to the amplitude, the duration of the state without any motion, there is a larger range, which is presumably due to environmental conditions. Diagrams of real trajectories can be found in Harbich (2023a) and Yamaoka et al. (2016). It is idealized in

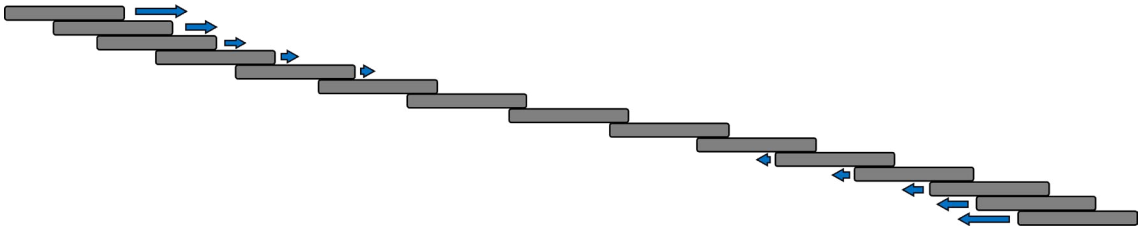

Fig.5. Small colony shortly after the start of movement from the resting state. The outer diatoms have moved inwards from the stretched state. The diatoms in the middle area do not yet show any relative movement.

Fig. 6a as a function of the phase of the oscillation. A laser-isolated cell has also been observed to move back and forth against the shard of its neighbor (Drum et al., 1971). When we ablated *Bacillaria* cell #2 with a pulse ruby laser, as described above, cell #1 oscillated against the shards of cell #2, but what is perhaps of importance, the rest of the colony sped up greatly, and drifted out of the FOV (Field of View). Between Cohn et al. (1999) and light variations from waves above benthic diatoms (Tanabe et al., 2020), we now have indications of rapid responses of diatoms to light changes.

The gray areas indicate the period in which the positions become stationary. Its duration was chosen to be 1/10 of the entire period. In nature, there is a larger range in which this time span can lie.

Fig. 6b shows the displacements of a *Bacillaria* colony, assuming a constant phase shift for illustration purposes, which only applies approximately in nature. If we consider a colony of only five diatoms, their movement is described by four displacements. These are marked by the black lines in Fig. 6b. Due to the displacements, there is now a narrow region (gray bar) in which all displacements are constant over time. If the colony is enlarged by three diatoms (green lines), this region disappears completely. The chain does not have a state with a finite rest period. In the last step, the colony was further extended by additional diatoms (red lines). This results in two time windows with opposing movements within one period. In these regions, some diatoms are still moving towards the resting state at maximum displacement, while others have already begun to move in the opposite direction. In general, opposite movements occur if the sum of all phase shifts becomes bigger than the phase that corresponds to the duration of the rest period. If the sum of all phase shifts reaches the value π, then there is for each diatom another diatom that moves in the opposite direction. Larger synchronous colonies thus exhibit more complex forms such as multiple S-shaped structures, as already described by the discoverer of the species, the Danish zoologist Otto Friedrich Müller (1782), translated in Ussing et al. (2005).

Furthermore, the movement of large colonies shows clear irregularities. In particular, global synchrony of movement no longer occurs. The further apart diatoms are in the chain, the less often they move synchronously over longer periods of time.

It should be mentioned that local mechanical stimulation, for example with a brush hair, can lead to a rapid autonomous reaction of a large number of diatoms. A stretched smaller colony can thus be brought to a rapid contraction. This is described by G. Funk (1919) and Kapinga (1989).

Modeling the movement

A communal signal that synchronizes the *Bacillaria* colonies has not yet been found. A rapidly spreading signal is not easy to reconcile with the observed phase shift and the opposing movements.

For the movement of diatoms, a description by oscillators and cell-to-cell communication was proposed early (Kapinga and Gordon, 1987). Such a model requires only the sensing system mentioned in the film, but no global clock or signaling across several cells.

A mathematical modelling of the synchronization of the movement by coupled oscillators, which are localized at neighboring coupled raphes, leads to a phase shift of the adjacent movements within the framework of the Kuramoto model, if one assumes that there is a time delay due to transport and processing of the information about the position of the diatoms (Harbich, 2023a). In the case of a steady colony, the movement starts from the ends (Fig. 5) without any additional assumptions. The maximum size of a synchronously moving colony results from the coupling strength of the oscillators. For larger colonies, the model shows local temporary synchronization effects. The model also explains the observation (Yamaoka et al., 2016, Harbich, 2023a) that diatoms in advanced division lead to separately synchronized sections of the chain and zig-zag shapes. Further modelling of *Bacillaria* has been carried out by Alicea et al. (2021) and Alicea et al. (2023).

Finally, it should be mentioned that the movement of the colonies can be synchronized by a slowly varying periodic light. Whether the external light is distributed in a kind of light guide in the colony has not yet be decided. In particular, one hypothesis for the partial synchronization of *Bacillaria* is that light is transmitted along the chain of cells:

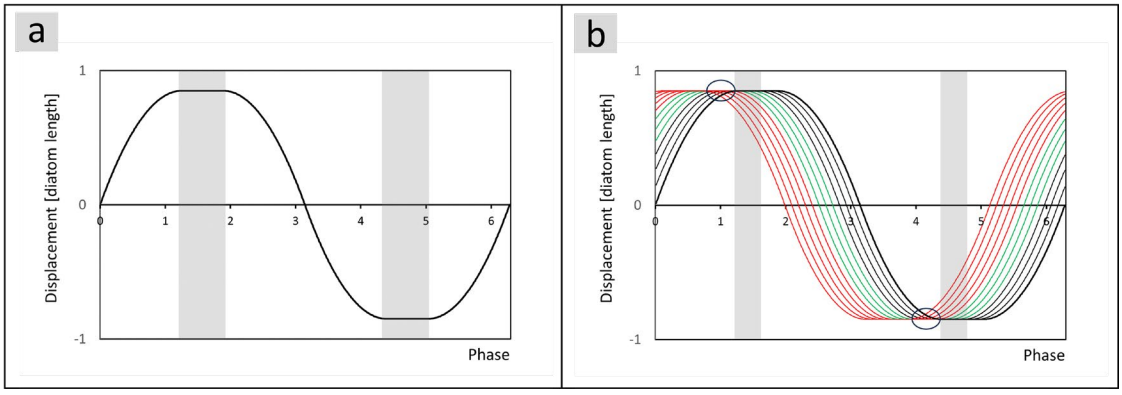

Fig.6. a: Idealized curve of the displacement over the phase. The corresponding period lasts approximately 60 seconds. The apical length of a diatom was chosen as the unit of length. **b**: A phase shift of 1/60 of the period is assumed between neighboring diatoms. In real colonies the phase shifts are usually smaller. The two regions where opposite motions occur when all diatoms are present are outlined in black.

"The resting stage involves alignment of all the cells in a stack with no obvious mechanical stop (Ussing et al., 2005). Given that there is a photosensitive region at the distal ends of a pennate diatom, which causes the diatom to respond to a 'light wall' by reversing direction (Cohn et al., 1999) we would like to hypothesize that a light pipe forms between these photosensitive regions when the cells are stacked. It might be responsible not only for the aligned resting stage but also for the partial synchrony of movement of the cells" (Gordon et al., 2009).

While this hypothesis may not be consistent with other observations, it has not yet been tested directly by using a fiber optic to put light in one end of a colony and seeing where it comes out, or its effects. An obvious advantage would be to supply any whole colony with light, especially when partially embedded in sediment. The successful experiment on the synchronization of *Bacillaria* movement in a slowly varying periodic light field (Harbich, 2023a) supports this hypothesis.

Continuing thoughts on the movement of Bacillaria paradoxa colonies

Because the velocities are additive, this is the "world's fastest microorganism" (Drum and Gordon, 2003), at least when all cells are all moving in the same direction.

While Jeremy's Pickett-Heap's section on motility is visually intriguing in regard to coordinated movements inside and outside of a raphe, there is the need for light microscopy cloaking (Ghobara et al., 2019) to better see what is going on under a valve. Hypotheses such as the existence of raphan and raphan synthase (analogous to cellulose synthase), hypothesized to move under an oscillating electric gradient in the cell membrane, and the molecular concerted movement of raphe fibrils (Raj Vansh Singth et al., 2023), stemming from a review of the many models for diatom motility (Gordon, 2021), need investigation, and less complicated molecular modelling.

The flow of water around a moving diatom has preliminarily been investigated by PIV (Particle Image Velocimetry) and suggested anomalous viscosity (Ali Beskok and Can Sabuncu, personal communication, 2019). This could have impacts on the design of faster ships. How/when the raphe fluid gets past the hyaline center of a raphe is unknown.

Cohn's work on light detecting spots at the ends of motile diatoms needs ultrastructure and molecular work (they have a distinct spectral sensitivity, different from photosynthesis). They might be involved in the light piping hypothesis for synchronization of *Bacillaria*, which needs testing for colonial diatoms. The spots could be involved in synchronization or light distribution to all cells in other colonies of attached cells.

Bacillaria form a cloud of raphe fluid around them, barely visible via the detritus in it (Rines, 2001). Whether this plays a mechanical or other role in motility is unknown.

Three species of *Bacillaria* have been identified (Schmid, 2007; Jahn and Schmid, 2007).

Phylogenetic notes on motility in diatoms

With regard to mobility as discussed in the film, it should be noted that *Ardissonea*, despite the elongate shape of the frustule, is more closely related to the radially-symmetrical diatoms of the Mediophyceae than any bilaterally-symmetrical clade (Medlin et al., 2008, Lobban et al., 2022). Motility similar to that exhibited by *Ardissonea* has also been documented in a sister genus to *Ardissonea—Toxarium* (Kooistra et al., 2003).

As for the hypothesis proposing the labiate process might be a precursor to the raphe slits of the Bacillariophyceae, the molecular data are still ambivalent. While there is a fragilariophycean genus with a series of labiate processes which open into a single, slit-like canal at each valve apex (*Pseudohimantidium*), DNA sequence data from these diatoms suggest that, rather than being sister to the raphe-bearing Bacillariophyceae, these are sister to a derived group of fragilariophyceans within the order Cyclophorales (Gómez et al., 2018); this order includes the aforementioned genus *Astrosyne*. A similar morphology exists among the raphe-bearing diatoms of the Eunotiales, where the raphe slits are small and restricted to the apices of the valves. However, these diatoms also possess labiate processes near the valve apices, suggesting that labiate processes and raphe slits are independent structures. Even the earliest molecular phylogenetic studies failed to resolve the Eunotiales as sister to all other raphe-bearing diatoms (Medlin and Kaczmarska, 2004), a pattern that has continued as taxon sampling and sequencing breadth have increased (Theriot et al., 2015, Nakov et al., 2018).

Movement along Actin Cables generated by myosins

It is demonstrated in the film that the cytoplasmic streaming underlying the raphe occurs at the same speed as whole cell transport, and reported that this transport is generated by the adjacent actin filaments. It was also reported that cell movement was generated by «mucilage secretion coupled with cytoplasmic transport». A more likely possibility and more accurate description is that both the cytoplasmic transport of organelles and the force for mucilage-based cell movement is generated not by the actin in the cell, but rather along the actin cables present, using specific actin-based motor proteins such as the plant-specific myosin XI known to generate a wide variety of plant and algal based organelle transport (Buchnik et al., 2015; Kurth et al., 2017; Duan and Tominaga, 2018; Davutoglu et al., 2024). These proteins can generate movement of about 5-10 μm s^{-1}, although in some species can be up to 50 μm s^{-1}. Thus, the similarity in speeds in the two processes of cytoplasmic transport and cell motility may be due to force generation by the same molecular motors.

2.6. Note on Chapter 10 "Phototaxis"

Photo-regulated movement regulated by biasing direction change at light boundaries

As photosynthetic organisms, diatoms require light for energy production. However, like many algae, the cells are sensitive to the levels of light to which they are exposed, with excessive illumination being harmful. For instance, overly high irradiance can damage diatom photopigments (Cartaxana et al., 2011), and recent

studies with fluorescein staining of siliceous valves have shown that the additional light from fluorescent valves can degrade diatom chloroplasts (Annenkov et al., 2024). While diatoms have evolved physiological mechanisms to protect from over-exposure (e.g. some diatom valves contain special mycosporine-like amino acids which help protect cells from UV radiation; Ingalls et al., 2010), the motility of diatoms, in which they migrate and collect in areas of optimal illumination as shown in the video, is likely an additional important adaptive survival strategy. The frequency and intensity of light which triggers such optimal cell accumulation seems to be part of a species-specific well-regulated response, in which different diatom species are triggered by different light conditions (Cohn and Weitzell, 1996, Cohn et al., 2016).

The characteristics of movement responses relative to light frequency and light intensity have now been characterized in several species (see e.g. Cohn et al., 2021), and seem to indicate that light drives diatom movement and accumulation/dispersion by regulating the enhancement or repression of direction changes in their movement (Cohn et al., 2015). It has been discovered that not only do different species respond quite differently to different intensity and wavelengths of light, but have motile behaviors that can be modulated by the presence or absence of other species (Cohn et al., 2016). In this way, diatoms are able to accumulate into areas of appropriate light (e.g photosynthetically active) by changing direction at the approach from light into a dark boundary and out of inappropriate light (e.g. high intensity damaging light, or not photosynthetically active) by changing direction when moving into the light. The light sensitivity is thus not really phototaxis in the classical sense of plant movement, but rather considered to be a photophobic response in which cells are not driven to move toward the light, but directionally biased to avoid the light by regulating the frequency of direction changes when cells encounter boundaries with different light conditions. This is likely the reason that *Pinnularia* spp., which typically have mainly circular paths of cell movement, and therefore limited areas of cell exploration, have much more limited rates of cell accumulation into light. This light-dependent localization effect, which is species-specific, coupled with the modulation in the presence of other species, can help give rise to niche partitioning of the diatoms, in which species become localized and more ecologically successful within a complex algal community.

2.7. Notes on Chapter 14 “Mitosis and Cleavage”

Zig-zag shaped colonies

The zigzag-shaped colony shown (presumably created by diatoms of the genus *Tabellaria*) is described with the words: “These zigzag colonies result from adhesive plugs on opposite corners.” In fact, it is remarkable that the diatoms and parallel connected diatoms in girdle band view form approximate rectangles, which are connected at the opposite corners with a pad of extracellular polymeric substances (EPS). Although this pattern of EPS pads is very common, it should be noted that as the colony continues to grow, it inevitably leads to constellations in which the EPS pads are not opposite each other (diagonal) but are arranged on the same apical side (non-diagonal).

Chain-shaped clonal colonies are formed when diatoms remain connected after cell division, for example by mucilage, for a time that is significantly longer than the generation time (Tiffany et al., 2010; overview of forms in Rimet and Bouchez, 2012). Zigzag-shaped as well as star-shaped colonies develop in pennate diatoms when they fold apart after cell division but remain connected to the neighboring diatom close to an apex. Depending on the species, this splitting into a V-shape does not always occur immediately after the morphogenesis of the valves. Diatoms can also remain connected valve to valve in a parallel arrangement for long periods of time, allowing further cell divisions to take place before splitting. In this case, groups of unseparated diatoms are observed in addition to individual diatoms in the chain or turbulence.

The splitting of parallel diatoms after completed cell division is a random process. Considering a single diatom, the minimum time from its formation to the subsequent separation is given by its doubling time. In principle, it cannot be excluded that the probability of separation also depends on the position in a chain.

A nomenclature introduced by Harbich (2023b) is used to describe the various possible connections.

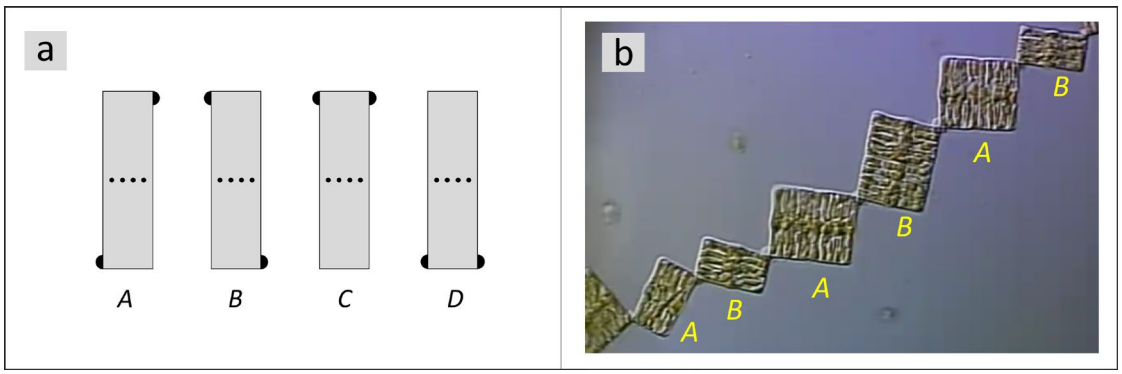

Fig.7. a: Types of possible patterns of adhesive pads on a diatom or a parallel connected group of diatoms, **b**: Assignment of types to the colony shown in the video (Pickett-Heaps, 2003).

Imagine a zig-zag shaped colony in horizontal position and girdle band view and assign a specific type to each possible arrangement of connection points to neighboring diatoms or groups of diatoms as shown in Fig. 7a. The dots indicate that it can be one diatom, or several diatoms connected at the entire valve. For this reason, capital letters have been used in contrast to the characters chosen in Harbich (2023b). The notation refers to a fixed view of the chain. The transformation of the symbols for rotations and mirroring results from the symmetries of the defined elements. The elements *A* and *B*, where the connection points are opposite each other, should be named "diagonal", *C* and *D* "non-diagonal".

The connection pattern of a chain is characterized by a sequence of characters from {*A*, *B*, *C*, *D*}. The notation of the chain in the video (Fig. 7b) is *ABABAB*. As the blocks at the edge of the image cannot be unambiguously assigned to a type, they are not included in the formal description. For easier identification, it is recommended to place the chain horizontally and imagine that the angles between the diatoms are reduced. Also note that *A* can only be followed by a *B* or *C* and *B* can only be followed by an *A* or *D*.

If elements *A* or *B* are split, the newly created connection point can occupy two different positions. This results in processes I to IV in Fig. 8.

In all cases, one non-diagonal element is created. A colony or a part of it is therefore not permanently connected by connecting points at opposite corners. The position of the connection points is determined by the excretion at the ends of the poles and is fixed before detachment. When this non-diagonal element separates, the processes V to VIII shown below in Fig. 9, occur.

Given the dominance of diagonal elements in some colonies, processes VI and VIII appear to be absent or rare. In *Diatoma vulgaris*, for example, only processes V and VII are observed after cell division. In addition, in this example the separation of a non-diagonal element takes on average less time than the separation of a diagonal element. Obviously, chains of diagonal elements are dominant when:

- the non-diagonal elements *C* and *D* separate into diagonal elements and
- the average duration of the separation of non-diagonal elements is small compared to the average duration of the separation of diagonal elements.

Starting from a diagonal element, one then typically observes the sequences of processes shown in Fig. 10.

Two successive processes replace *A* with *ABA* and *B* with *BAB*. At a later stage, the diagonal element formed during the first separation splits. In the case of non-diagonal bundles of several parallel diatoms, longitudinal tensile forces may play a role in favoring separation into an AB structure, if this possibility exists due to existing connection points.

Role of motor proteins in regulating cell division

The film shows the dramatic movement of the microtubule center during a typical cell cycle, with its localization near the nucleus during interphase, and migration to the site of spindle formation during the nuclear breakdown and onset of mitosis, often moving a considerable distance in the cell to a new site, now adjacent to the formation of the developing mitotic spindle. While the diatom (and many other algae) has a microtubule organizing center that is devoid of the typical animal cell structure of centrosomes containing centrioles, the described behavior of the centrosome is completely analogous to animal cell centrosomes, in which the movement of the centrosome is driven by the coordinated activity of cellular motor proteins. These motor proteins (mainly kinesins and dyneins) along with associated cellular attachment sites and the attachment of other components to the microtubules emanating from the organizing center, drive the placement of mitotic spindles in many eukaryotic organisms (Karsenti et al., 1996; Marc J, 1997). The microtubule in diatoms is thus not an exception, but rather a typical example of the general way centrosomal-like organizing structures containing γ-tubulin help to coordinate the proper placement of mitotic spindles prior to cell division.

Numerous studies have help to solidify the role and importance of kinesins in the elongation of the spindle during anaphase, for not only the diatom central spindle but among a diverse range of eukaryotic organisms (Wein et al., 1998; Avunie-Masala et al., 2011; Krüger et al., 2021). Drug perfusion studies have also helped elucidate the energy requirements for spindle elongation and microtubule center movement after division. Addition of dinitrophenol (an ionophore that rapidly eliminates mitochondrial ATP formation) quickly stops spindle elongation in *Surirella* spp. as well

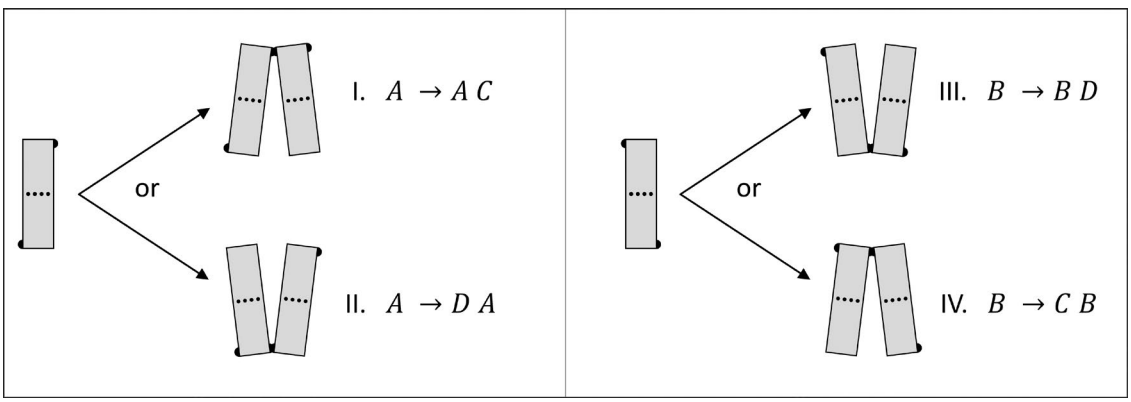

Fig.8. Possibilities for separations of diagonal elements.

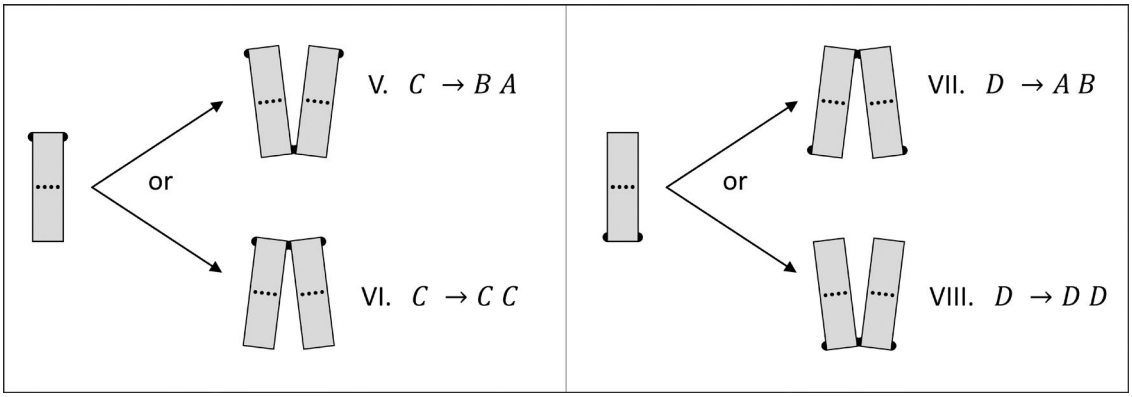

Fig.9. Possibilities for separations of non-diagonal elements.

as the localized movement of the microtubule center (Cohn and Pickett-Heaps, 1988). Addition of the microtubule poison colchicine also eliminated the movement of the microtubule center to the corner of the cell following mitosis (seen also in chapter 15 of this film), causing dramatically abnormal cell wall formation in the daughter cells (Cohn et al., 1989a). It is clear that the proper movement and activity of the microtubule organizing center during mitosis is crucial for spindle placement and subsequent valve formation.

2.8. Notes on Chapter 15 "Valve Morphogenesis"

Role of osmotic pressure in Valve Morphogenesis

A recent study revisited the influence of osmotic pressure on valve morphogenesis, where the authors exposed multiple strains of the mediophycean diatom *Pleurosira laevis* to varying salinities (Kamakura et al., 2022). Two forms have been documented in this diatom: one with flat valves and one with convex valves. These two forms have been described as unique taxa and unique forms of a single taxon, and "Janus cells" (frustules with one flat valve and one convex valve) have also been documented. While environmental cues have long been suspected to have some significance with regard to these two forms, Kamakura et al. (2022) documented the changes wrought on the valve shape by salinity in both strains originally isolated from marine environments changing from a convex valve to a flat valve in freshwater media, but also strains isolated from freshwater environments changing from flat valves to convex valves when exposed to saline media. The authors suggested that this is most likely the consequence of osmotic pressure influencing the shape of the cytoplasm as the new valves form after mitosis.

Cytoskeletal components and biochemicals used in regulation of Valve Morphogenesis

The requirement of cytoskeletal components for proper valve morphogenesis was further substantiated by treatments of diatoms during early valve formation with drug inhibitors of microtubules or actin (Bedoshvili et al., 2018, Bedoshvili et al., 2023). Such treatments showed that inhibition of microtubule formation early in valve morphogenesis resulted in either the very abnormal placement of valve components (as in *Surirella* spp.) or abnormal raphe formation (as in *Pinnularia* spp. or *Hantzschia* spp.). Treatment with an actin inhibitor also inhibited the transport of newly formed valve components to the edge of the cell in *Hantzschia* spp, causing a raphe canal to be developed on the surface of the valve face rather than in the corner of the frustule (Cohn et al., 1989a).

Monitoring of valve morphogenesis, starting from the formation of primary silicon-containing particles, is possible using the fluorescent biosilica trackers mentioned above (Table 1). In particular, submicrometer-sized cytoplasmic silica particles (Annenkov et al., 2013) were detected, and the formation of the silica deposition vesicles was visualized by video (Annenkov et al., 2019). Fluorescently tagged poly(acrylic acid) was used as a model of oligosilicates to test the pinocytosis hypothesis for silicon capture from the environment (Annenkov et al., 2020). Fluorescent vital dyes capable of staining growing siliceous structures have been actively used in works dealing with cytoskeletal action, growth of new valves, etc. The development of new technologies in microscopy, including overcoming wavelength limitations, will lead to new discoveries based on vital biosilica trackers.

2.9. Note on Chapter 16 "Spine Morphogenesis"

Many different structures have been called "spines"

Much like the terms "centric" and "pennate", the term "spine" is purely descriptive and should not infer any sort of ontogenetic or evolutionary homology. Williams (2019) pointed out that, even within the Fragilariophyceae, structures called "spines" can

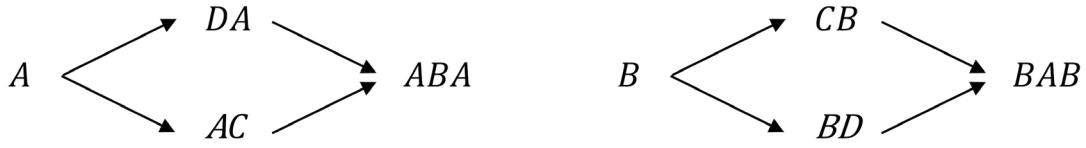

Fig.10. Two successive divisions, starting from an element of type A (left) and an element of type B (right).

have significantly different ontogenetic histories (such as arising from virgae or vimenes of the developing valves) and cannot be considered homologous. In the case of the "spines" mentioned in the video, some are actually the external tubes of the labiate process, and subject to different morphogenetic processes than, for example, the mantle "spines" of *Corethron*.

The noted differentiation between *Rhizosolenia* and *Proboscia* based on the presence or absence of a labiate process at the peak of the valve center has been shown to be slightly more nuanced than presented. Jordan et al. (2019) illustrated the "spines" of several *Rhizosolenia* and *Proboscia* spp. under SEM, documenting several different internal morphologies of the labiate process at the base of the "spine" (representing the external tube of the labiate process) in various *Rhizosolenia* species. In the broken valves of several strains, they also documented that a labiate process exists near the tip of the "spine" in *Proboscia*, expressed externally as a slit and internally as two thin, rounded siliceous slabs. Thus, the labiate process is involved in the "spine" of both genera, though in *Proboscia* the labiate process is borne by the "spine", rather than the labiate process being the "spine" in *Rhizosolenia*.

In DLA (Diffusion Limited Aggregation), growth of structures follows spatial chemical gradients, due to the local depletion of the precipitant. The setae of diatoms, in their curvatures, look much like they follow such gradients. To test this, we propose altering the supposed silica gradient by flow and/or saturation.

2.10. Notes on Chaps. 20 "Sex in Pennates"

Gamete diversity in "centrics" and "pennates"

The mechanisms of sexual reproduction in diatoms have been shown to be far more diverse than was understood at the time this video was produced. Davidovich et al. (2017) documented gametes in the mediophycean diatom genus *Ardissonea* with motility driven by amoeboid cytoplasmic extensions, rather than the flagella expected in a "centric" clade. The sexual reproductive cycle in *Ardissonea* remains anisogamous, as the amoeboid motile gamete is significantly smaller than the immobile gamete. Among the araphid "pennate" diatoms, a somewhat similar anisogamous sexual cycle was described in *Pseudostaurosira* (Sato et al., 2011) and *Plagiogramma* (Kaczmarska et al., 2017). Rather than featuring numerous amoeboid pseudopods, as in *Ardissonea*, the motile gametes of *Pseudostaurosira* appear to maneuver via an elongated pseudopod. While gamete ultrastructure has only been described in a small fraction of the overall diversity of diatoms, mapping the known sexual cycles to the molecular phylogeny appears to support a narrative of an overall evolutionary trajectory from anisogomous gametes with flagellate motile gametes, to anisogamy with amoeboid, pseudopod-bearing motile gametes and finally to the isogamous, amoeboid gametes of the raphe-bearing "pennate" diatoms.

Size regeneration, auxospore ultrastructure and the molecular phylogeny

With regard to the auxospore and size regeneration in diatoms, it should be noted that one level of the classification based on the molecular phylogeny proposed by Medlin and Kaczmarska (2004) has continued to be monophyletic in nearly all subsequent analyses, regardless of taxon sampling and marker: the Bacillariophytina. This clade includes the "centric" Mediophyceae and the "pennate" Fragilariophyceae and Bacillariophyceae, and appears to correspond to the evolution of perizonial bands, which shape the immature auxospore into the elongate and prism-like mature cells. Whether or not further taxonomic diversification correlates to the diversification of perizonial bands seen across the subdivision Bacillariophytina will require further documentation of the early and immature auxospores from additional taxa.

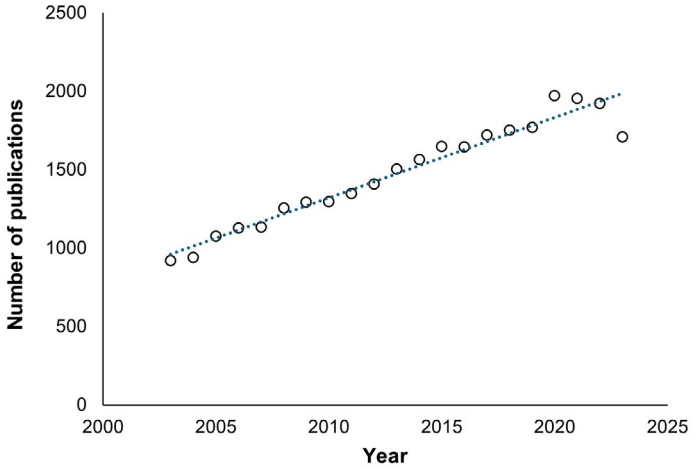

Fig.11. Publication records spanning the past two decades since the release of Picket-Heaps' instructional video "Diatoms in Glass Houses," extracted from the Web of Science Core Collection (webofscience.com) using the keyword "diatom" across all publication types.

The "uncanny symmetry" (Pappas et al., 2021) of some diatom valves has yet to be explained. It might be related to polygonal shapes in many Archaea (Gordon, 2024), which has a possible explanation in energy minimization of the S-layer.

Diatom pheremones in sexual reproduction

One of the key questions in diatom sexual reproduction is the nature of how individuals from potential mating pairs find each other prior to alignment, secretion of the protective mucilage coat, initiation of meiosis, and migration of the gametes for fusion. Recent work has pointed to the presence of diatom pheromones that act as sexual attractants during sexual reproduction (Bondoc et al., 2016; Moeys et al., 2016; Klapper et al., 2021). These investigations also suggest that the pairwise association is driven by compatible mating types, with one mating type acting as a relative stationary cell secreting an attractant for cells of the other mating type. Extraction of materials from cellular exudates showed ability to attract cells of the proper mating type. Diatom pheromones have also been indicated in the regulation of the cell cycle associated with meiotic gamete formation. The chemical nature of the pheromones in different diatom species is still under investigation, but in some species is thought to be related to proline derivatives such as L-diproline.

Cell Wall changes during sexual reproduction

In terms of valve morphogenesis after auxospore elongation, it has also been shown that the valve of the initial cell can have a number of distinct characteristics in pore and striation structure compared to the normal vegetative cells. These differences are true for both pennate raphid diatoms (Cohn et al., 1989b; Kaczmarska et al., 2000) as well as araphid diatoms (Sato et al., 2004). These differences are not surprising given the large amount of osmotic pressure derived cell growth and cytoplasmic reorganizations that take place in the auxospore prior to initial cell formation, that become stabilized upon vegetative growth. Studies are also currently underway (S. Cohn, personal communication) to measure the relative rate of cell size diminution during vegetative growth after initial cell formation.

3. Conclusions

In reflecting on the enduring legacy of the teaching video from Jeremy Pickett-Heaps, "Diatoms: Life in Glass Houses," published two decades ago, it is striking to witness how its content remains relevant to this day. Despite the modest size of the diatom research community and its relatively limited funding compared to other fields, the productivity and impact of this niche area have grown constantly, but not exponentially, over the years (Fig. 11). The advancements made in diatom research since the release of this video have been profound, touching upon various aspects of diatom biology, ecology, and biogeography. From investigating the molecular mechanisms behind frustule formation to exploring the ecological roles of diatoms in aquatic ecosystems, the field made significant strides in understanding these enigmatic microorganisms better. Moreover, the application of new imaging techniques and high-throughput sequencing technologies have provided deeper insights into diatom taxonomy and ecology, expanding our understanding of their diversity and functional traits.

As we dive into some updates and developments in diatom research following the sequence of topics presented in this video, it becomes evident that Picket Heap´s pioneering work laid a solid foundation for future investigations. From the utilization of diatomaceous earth in ancient construction to the exploration of photonic properties in diatom frustules for modern technological applications, the relevance of diatoms transcends time and spans across diverse disciplines. The intricate movements of *Bacillaria* colonies, the classification challenges posed by molecular techniques, and the fascinating intricacies of diatom motility serve the ongoing quest for knowledge and understanding in diatom research.

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Conflict of interest

The authors declare no conflict of interest.

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